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PROCEEDINGS
OF
The American Microscopical Society.

PARASITISM OF EPIPHEGUS VIRGINIANA.*

(Broom Rape, Cancer Root.)

Awarded First Prize in Plant Histology by the Society.

HERMANN SCHRENK.

Parasitism in General.

Discovery of Parasitism Among Higher Plants.

Pliny is the first to make mention of parasitic plants. He tells us of a wondrous plant (the Mistletoe) growing on oaks and other trees—a plant held in high esteem by the ancient Druids, who regarded it as holy, and used it to a large extent in their religious ceremonies. The Arabs of the tenth century had a better idea of parasites than did the Romans or even the Europeans of the middle ages. In the writings of the Lautere Brüder (18)† we find the fol-

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† NOTE.—The figures refer to the bibliography at the end of the paper. Particular references are there given to volume and pages, except in the case of references of a general nature.

lowing: "Among the plants there is still another kind which in its action represents the animal soul, while its body is a plant, for it has neither a fixed root nor leaves, but fixes itself to trees, crops, and thorns, and sucks moisture; it nourishes itself from them as the worm does, which crawls on leaves and plant stems, sucks from them, cuts them, eats them; in short, feeds on them."

History of Classification of Parasites.

In the middle of the seventeenth century a new era began for the study of these plants, partly because of the discovery of new species, and partly from a better knowledge of the ones already discovered. In 1789 Pfeiffer (56) makes three divisions of parasitic plants according to habit: 1. climbing ones, as *Cuscuta*, *Rhus*, etc.; 2. such as grow at one point on trees, such as *Viscum*, *Arceuthobium*; 3. on roots, as *Monotropa*, *Orobancha*, etc. He advanced the idea that parasites were not individual plants, but were simply evidences of a deceased sap of the plant on which they grew.

In 1832 A. de Candolle (13*b*) devoted several chapters in his *Physiologie Végétale* to the consideration of parasites and saprophytes. He writes: "If we examine the actions of plants living one upon the other we will nearly always find them in a state of war, more slow and less apparent, it is true, than that of animals or men among each other, but continuing and very important in its results." He divides true parasites into two large classes, those living inside the host, and those living outside. The latter are either Phanerogams or Cryptogams. The following is a scheme of his classification:

<i>Phanerogamia</i>	{	<i>Chlorophylles</i>	<i>Loranthaceæ</i> .
		<i>Radicules</i> or	<i>Cytineæ</i> , etc.
	{	living on	Polyrhizes... <i>Monotropa</i> , etc.
		roots.	Polystomes... <i>Lathræa</i> , etc.
<i>Cryptogamia</i> .	{	<i>Aphyllæ</i>	<i>Cuscuta</i> .
		<i>Caulicoles</i> or living on	
		stems.....	

On morphological grounds Unger (74) divides them into nine classes (*i. e.*, according to method of attachment). Martius (45) makes four classes: 1, leafless, colorless; 2, colorless on stems (caulicoles); 3, leafy green with primary roots on host; 4, green with secondary roots on host. Hallier says (31): "There are two kinds of parasites. The first produce no chlorophyll and take all

their nourishment from their host (Orobanchaceæ), the others assimilate partly (Mistletoe, etc.). Edmunds (21) divides them into—*a*, semiparasites; *b*, green parasites; *c*, perfect parasites.

The latest classification is that of Johow (36). He divides, first, into *autoxene*, growing on one host only, and, second, *metaxene*, growing on more than one host during their life history. The former are divided into, 1. *euphytoid* parasites, upright ground plants; 2. *lianoid* parasites, climbing ones; 3. *epiphytoid* parasites, on trees; 4. *fungoid* parasites. To the first division five families with thirty-five genera and four hundred species belong. Most of them are green, as the Santalaceæ and Scrophulariaceæ, but many are colorless as the Orobanchaceæ. To the second class belongs the genus *Cuscuta*, with seventy-seven species, and the obligate hemiparasitical genus *Cassytha*, with about twenty exotic species. To the third only obligate hemiparasites belong, five hundred species of Loranthaceæ and fifteen to eighteen antarctic Santalaceæ (*Henslowia*, *Phacellaria*, and *Myzodendron*). These are mostly upright shrubs with well-developed leaves. Among the Fungoid he groups the Balanophoreæ with about twenty-three species.

In all Johow says there are about one thousand dicotyledonous parasites. It is a curious fact which might be noticed that nearly all phanerogamic parasites are dicotyledonous, and are parasitic, as a rule, on dicotyledonous plants. To this there are however some exceptions—*i. e.*, species of Dodder (*Cuscuta*) growing on various grasses. An explanation for this might be that, as a rule, the monocotyledons have their vascular parts more toward the inner portion of their stems, for they are scattered and not so liable to be hit upon by a haustorium, and again they are more often protected by a more or less hard and resisting epidermis, silicious in many cases.

At any rate they present more difficulties to the haustorium than do the dicotyledons.

Definitions of Parasites.

There has been much discussion from the earliest times as to the true meaning of the term parasite and the extent to which it ought to be applied. A constant clash has existed between it and another term, saprophyte.

The earlier writers, as Pfeiffer (56), considered parasites as dis-

eases. Later ones included such plants as *Rhus*, *Tillandsia*, etc., among them, and even now a true and accurate distinction between a parasite and saprophyte is impossible.

De Bary (17) says: "Parasites (referring mainly to fungi) are such as feed on living organisms, whether plant or animal. Their relationship with their hosts is that of a common life, a symbiosis." Saprophytes he defines as such living on decaying bodies and feeding on dead organic matter. He then goes on to show that these may be sharply separated, excepting certain forms. "There may be species," he says, "which both can and do normally go through the whole course of their development as saprophytes, but which also have the power of going through their course of development wholly or in part as parasites; these may be called facultative parasites. Secondly, species which, as far as we know, do, as a rule, go through the whole course of their development as parasites, but at the same time are able, at least in certain stages, to vegetate as saprophytes; these may be called facultative saprophytes." Accordingly, he classifies all these plants with respect to their life condition into—1. pure saprophytes; 2. facultative parasites; 3. obligate parasites (plants to which parasitic life is indispensable to full development of their functions).

Dr. Farlow (22) says the following: "A parasite is usually defined as a plant which is unable to transform inorganic material into organic compounds, and which is consequently obliged to obtain its organized materials from other plants or from animals. The definition in general is an accurate one and correctly defines the vast majority of vegetable parasites which belong to the class of fungi. . . . Of the parasites we have two kinds: 1. the saprophytes, which live on dead or inert matter, and, 2. the special or true parasites, as they are usually called, which can only grow on the tissues of living plants or animals."

From the above there will appear to be great difference of opinion as to these two terms, but in reality they all agree in saying that parasites are such plants not assimilating carbon dioxide, which get their nourishment from living plants, while saprophytes are such plants not assimilating carbon dioxide, which get their nourishment from dead or dying plant matter.

Constantly forms supposed to be true parasites are found to be saprophytes. *Monotropa* is a good example. *Melampyrum* and

Rhinanthus, formerly considered true parasites, but whose nature as humus inhabitants is now beyond doubt, may be considered as transitional forms between parasites and saprophytes.

Parasites from a Physiological Standpoint.

No doubt the most interesting point of view from which to study parasitic plants is the physiological one. With it some of the most vital questions in plant physiology are connected and too little is known of them.

Parasites may be considered according to the amount of support they receive from a host, hence different grades of parasitism may be distinguished. *Gerardia* and plants closely allied to it present the first grade. These plants take the larger part of their nourishment from the soil by means of true roots. They have green leaves and breathe carbon dioxide, yet they are attached to roots of other plants and take nourishment from these. The mistletoe goes a step further. It has found that it is a great deal easier to have the tree do its absorbing for it than to do it itself. An interesting experiment was performed, showing that the mistletoe does not have sufficient power to draw water into its tissues. A branch of mistletoe was put into water, and the water was measured and found not to diminish, no matter how long the branch remained, but when a piece of the branch of the tree to which the parasite was attached was put into the basin water was rapidly absorbed. Plants of the character of *Orobanche* form the last link in the chain; they take all their nourishment from their host. Lory (42) has made an extended investigation concerning respiration of the *Orobanchaceæ* as a type more or less of colorless parasites. His results show that these plants breathe oxygen and exhale carbon dioxide.

Orobanchaceæ.

The *Orobanchaceæ* is an order of plants the members of which have been known for a great many years. The Greek historians tell of plants which destroyed large areas of their crops, and the Romans contended with some of them. The name of the order is derived from two Greek words, *Orobos*—vetch and *ancho*—to strangle, applied by Dioscorides because the species were supposed to kill the plants upon which they grew.

The order is widely distributed all over the world, although, as a rule, they are found chiefly in temperate climates. The distribution of the genera is rather striking. The genera *Epiphegus*, *Aphyllon*, and *Conopholis* are characteristic of North America; *Christisonia* inhabits India; *Phacellanthus* occurs in Japan and the neighboring islands, while *Aeginetia* grows in tropical and subtropical Asia. The largest genus, *Orobanche*, is scattered all over the world; the majority of its species, however, occur in Europe. In the whole order there are about one hundred and fifty species, of which there are approximately one hundred belonging to the genus *Orobanche*.

The Orobanchaceæ are true parasites, receiving their nourishment from their hosts. There is however some doubt with regard to this, as is shown by Pfeiffer (55), who said in 1881: "It is true that the parasitic Orobanchaceæ take food from their hosts, yet a little is produced by decomposition of carbon dioxide, and finally the roots which spread around in the soil certainly take water, probably ash constituents, and perhaps organic matter."

The order is the one hundred sixteenth in Bentham & Hooker's *Genera Plantarum*. Eleven genera are described in that work and about one hundred and fifty species are enumerated. The order may be characterized as follows: Leafless herbs, variously colored, never green, and parasitic upon roots. The stem or scape springs from a scaly base, is short or elongated, simple or branched, the branches densely crowded with alternate sessile scales; the upper branches bear the flowers. The flowers are either single in axils of the scales, sessile, or with a peduncle, or crowded into dense terminal spikes; the flowers hermaphrodite (dimorphous in *Epiphegus*) and irregular; calyx inferior, $\frac{4}{5}$ toothed or lobed; corolla gamopetalous, tubular, and generally more or less two-lipped, ringent, the upper lip entire or two-lobed. There are four didynamous stamens attached to the tube of the corolla below the middle, alternate with the lobes, often included, more often extruded; anthers, two celled; ovary superior, usually attached by a broad base, one-celled, two-valved, with parietal placenta; style terminal, carrying a rather large stigma often obscurely two-lobed, papillose above; placenta four, bearing numerous very small anatropous ovules. The capsule is more or less included in the calyx and dehisces pretty regularly in the middle, breaking into its two valves and scattering the seed. These are very minute, with an extremely rudimentary embryo.

*Epiphegus Virginiana.**Systematic.*

In studying the Orobanchaceæ the plant to which particular attention was paid is *Epiphegus Virginiana*. This plant is found in nearly all our beech woods, and is parasitic on the roots of the beech. It was first discovered in Virginia, and was given the name of *Orobanche Virginiana* by Linnæus (41). We find it mentioned as this in Pursh's Plants of North America (60); also in the work of Michaux (47). Nuttall was the first to point out the generic difference between Epiphegus and the Orobanches. In his work (51) he changes the name to Epifagus, from *epi*, "upon," and *fagus*, the "beech," because of its parasitic habit on the roots of the beech. It will be seen that this name is partly Greek and partly Latin. Rafinesque in 1819 denounces this name because of this fact, and proposed the name Leptamium (61), which, however, was not accepted, for in the same year that Nuttall published his work, *i. e.*, 1819, Barton (5) published the name *Epiphegus Virginiana*, from *epi*, "upon," and *phegos*, "beech." According to De Candolle (13c) Darlington, in *Florula Cestrica*, page 72, changed the name to Epiphegus in 1825, but Barton, preceding him, gave it the name it still holds, *i. e.*, *Epiphegus Virginiana*, Bart. The common names applied to it are Broom-rape, Cancer-root. The first is a term applied to the Orobanches in England because of their growing on the broom. The second has been applied in America because of its supposed healing action in cases of cancer.

Gross Anatomy.

The specific and generic characters of the plant are very marked, readily distinguishing it from all other Orobanchaceæ. On walking through beech woods in the late summer one will find brownish stems, destitute of leaves and bearing curious flowers in racemes, standing all about the beech trees. The lower part of these stems will be found attached to a root generally one-sixteenth to one-eighth of an inch in diameter, which can readily be traced to a beech tree. One must dig very carefully, taking pains to cut all around the stem, to cut every root; if one attempts to pull very hard the root will break off, the connection between host and parasite often being very small. After having removed all traces of humus and leaves, the plant will present a thick lower subterranean

stem and an upper branching portion bearing the flowers. The lower part bears upon it numerous curiously curved and twisted stiff outgrowths, or, as they have been termed, roots. Meehan (46c) has called these fibers, but I cannot agree with him in so calling them because of their great stiffness. They have been termed *grapplers*, and the name appears very appropriate, because they seem to grapple or seize anything within their reach. They originate at all points on the thickened portion, or rhizoma, and thus give the appearance of roots. They certainly are not branches, because not one of them comes from the axil of any leaf or scale.

The upper portion of the plant or true stem begins to branch very soon after it emerges from the earth; in many cases I have seen the branches start below the surface. In the rich humus of leaves in Delaware county, N. Y., I should say this was generally the case. Both the rhizoma and aërial stems have upon them rudimentary leaves in the form of scales. These are quite small, never more than one-fourth inch long. Their arrangement on the stem is five-ranked, *i. e.*, $\frac{2}{5}$. This is often very irregular, two scales being very near together and the next two farther off, giving an appearance of being opposite.

From the axils of these scales the flowers arise. They are in long extended racemes, one flower coming from each scale. *Epiphegus* is distinguished from other *Orobanchaceæ* by the possession of two kinds of flowers, fertile and sterile ones. The fertile ones are borne on the lower portions of the branches. The calyx is five-toothed and rather small. The cleistogamic corolla, which is very short, is forced from the base as the pod grows. The four stamens are very short and rather aborted, and surround the well-developed ovary, which is two-valved, with two parietal placenta on each valve. The sterile flowers (not always so, however) have a long, whitish and purple corolla, gamopetalous, irregularly five-lobed. There are four stamens, two long and two short ones, which are slightly exerted. The style is very long and bears a capitate stigma. The seed is very small, having an extremely minute embryo.

A variety *E. Virginiana*, Bart., var. *Rauana*, Austin (2), has been reported from the Catskill mountains. but does not appear to be well founded. Mr. Austin states that there are signs of malformation in the stamens, and the editor comments upon the fact that this would be the natural result of degeneration, *i. e.*, irregularity and sterility being the beginning in the degeneration. The sterile flowers are very rarely fertilized, while the lower ones are very fertile. In this

he sees a case of the general law that where plants have several methods of reproduction one is generally favored in exclusion or restriction of the other, the case here being the two kinds of flowers.

I have noticed a remarkable variety in this plant as regards the presence of the sterile flowers. In the rich humus in Delaware county the stems always had from one to twelve or fifteen sterile flowers on them. I do not remember seeing a single plant without them. In Six Mile creek and other places about Ithaca specimens were collected with no sterile flowers whatever. Indeed, the latter were rather the exception. In looking through several herbaria the same variability struck me, and I add a list of the specimens seen :

*Herbarium.**Where Collected.*

J. Torrey	New York	Sterile flowers present ; 8 on a branch ; 2 specimens.
Shuttleworth	Covington, La.	None ; 2 specimens.
Meisner herb	North bend near Ohio river.	Several sterile flowers ; 2 specimens.
Chapman, A. W.	Middle Florida	Several sterile flowers ; 2 specimens.
Morton, J. A.	Wingham, Ont.	None ; 4 specimens.
Morong, Thos.	Oradell, N. J.	None ; fertile ; very large ; numerous ; 4 specimens.
White, T. G.	Mt. Desert island ...	None ; 2 specimens.
Brown, Hon. A., etc...	Salt Pond Mt., Va...	None ; 3 branches.
Brown, Hon. A.	Hudson, N. Y.	None ; 1 specimen.
Brown, Hon. A.	New Dorp, S. I.	None ; 1 specimen.
Brown, Hon. A.	Closter, N. J.	2 sterile flowers ; 1 specimen ; 5 specimens : none.

(The above ex herb. Columbia College and ex herb. Hon. A. Brown.)

Fernald, M. L.	Orono, Me.	Several sterile.
Gray, Asa.	New Haven, Conn...	None.
Gray, Asa.	New England.	A good many.
Curtiss, A. H.	Bedford county	Enormous fertile pods ; 4-5 sterile.
Macoun, Prof.	Belleville, Can.	Small specimens, 3 ; no sterile flowers.

(The above ex herb. Harvard University.)

Hoy, D. F.	Delaware Co., N. Y.	Many sterile flowers present.
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These specimens will be seen to represent pretty well the Eastern range of the plant, and will show what variation exists.

On some of the specimens collected I have found some of the sterile flowers between the fertile ones about half way up on a branch; sometimes there were as many as six sterile flowers.

The coloring matter of the stem giving the purplish color seems to be dependent upon the light, indicating some affinity to chlorophyll. It has been held by some writers that reduced forms of chlorophyll were found in the epidermal cells of most colorless parasitic plants. In the epidermal cells, especially of the stem and branches of *Epiphegus*, numerous round bodies will be found very much resembling chlorophyll grains, but more dark brown. The color is extracted to a large extent by alcohol, for the plants which I put into alcohol soon turned pale and some nearly white, while

(NOTE.—For want of a better explanation of this variability I will present the following: The conditions for a large development of sterile flowers, so far as I have seen them, seemed to be a loose and moist soil, which might have offered better conditions for germination of seeds. In Delaware county, where there was a rich soil and easily permeable, it seemed that the conditions were extremely favorable for germination and development of seed, hence not requiring the production of so large a quantity in order to insure the survival and growth of a few. The non-formation of fertile flowers was necessarily followed by sterile ones. On the other hand, in Ithaca, where the conditions appeared more unfavorable (hard and dry soil), all the energies of the plant were devoted to formation of seed, in order to produce a large quantity, which would make the germination of at least a few more probable than if but a comparatively small number of seeds had been formed. On this account there would be very few, if any, sterile flowers. The same explanation might hold for the plants from Oradell, N. J. The spot where the plants grew is a picnic ground, in a beech grove, near the railroad station. The place is annually visited by a large number of people; the ground is tramped down; the bushes cut out; the soil is hard and scorched to a certain extent, making it far more difficult for a small seed to penetrate to the roots of the trees than would be the case in an undisturbed wood where the humus was light and full of interstices. The struggle for existence becomes intensified, and, as a result, a much larger number of seeds must be formed, to the exclusion of the useless sterile flowers.)

the alcohol became dark and finally nearly black. The stems growing in the soil, mostly branches of the parent stem arising from the rhizoma are, as a rule, snow white, and the transition to the purplish color above ground is very marked. The young plants which I found were entirely white, presenting a striking contrast to the black humus of the woods.

Physiology.

There seems to be a good deal of uncertainty regarding the life history of this plant, and especially in regard to its length of life. The plants begin to appear in July and live until the end of September or middle of October. In numerous works I find the plant mentioned as a perennial (60, 41, 136), while most authors say nothing at all about it. I do not wonder that it has been considered a perennial, for we find some enormous specimens of the plant (about 18 inches) with numerous branches. These are frequently found side by side with simple stems not 4 inches high. It hardly seems possible that such a large stem could be formed within a month. At the present time I am inclined to believe that the plant is not a perennial, but an annual. I have dug up a large number of plants this spring on Staten island and in numerous places around Ithaca, and without exception all were dead, the rhizoma being completely rotted. This was not only the case with the very large ones, but with all those having but one stem.

One argument which might be made in favor of its perennial character is the fact that a large amount of starch fills the cells of the rhizoma and grapplers in the fall. It might be said that this starch was stored there for use the next year ; but I think this is no evidence, for on examining the decaying rhizomas dug this spring (about the beginning of April) I found the remains of the cells full of starch, which gave the characteristic reaction with iodine. Why the plant should accumulate such a vast amount proportionately of starch in the fall only to let it go to waste during the winter is difficult to say. It might be explained by saying that, not knowing how much it was going to use, it kept on absorbing all it could get and storing it until far more was taken from the host than could possibly be utilized. Some of the dry branches examined had quantities of starch in them.

Epiphegus is a true parasite—that is, it derives, or apparently derives, all its nourishment from its host, the beech. This is true

at least of its mature state, the state in which I have studied it, and, judging from the closely related Orobanches, which have been so ably worked out by Koch (39c), it is parasitic throughout its whole life. Meehan (46c) says that he believes it to be dependent in its early stages, taking nourishment from the beech through a long thread or fiber. This takes place in the fall of one year. The next year he thinks the plant is independent, using the starch stored up during the previous year to produce flowers and fruit. This view appears to me to be erroneous, for every single plant which I examined was, while flowering, directly and plainly connected to a larger or a smaller root; and furthermore, I have never seen any plant which had no flowers at all, *i. e.*, one which would correspond to the vegetative stage of the first year. The older ones moreover may at once be proven to be parasites, because the roots to which they are attached are comparatively large, sometimes even three-sixteenths of an inch in diameter. These are so firmly held by the grapplers that there is little danger of the separation of the two plants, which might very easily happen, especially with young specimens.

To prove the attachment of the beech and the dependence of *Epiphegus* upon the latter, I carefully dug around several plants in the summer of 1892 at a distance of one foot, cutting all the roots. After a few days the plants, without exception, drooped, and after two weeks all were dead and dried up, thus proving that they were dependent upon some plant. Other plants of *Epiphegus* growing near by were perfectly healthy and remained so for six weeks after. Of the young stages of *Epiphegus* I have been able to get but one or two. While digging some of them in Delaware county I pulled out a seedling (one year old) of *Fagus ferruginea*, and to my great astonishment found a small *Epiphegus* attached to one of the fibrous roots of the seedling. The same is shown in a drawing on Pl. I, Fig. 2.*

Distribution.

The distribution of *Epiphegus Virginiana* is very limited, it being confined to the eastern United States and southeastern Canada. Its approximate range is shown by the accompanying map (Pl. X). In woods where it occurs it is generally very abundant, being found anywhere from close to the trunk to thirty feet away from it on either side, though most frequently near the trunk.

* In September, 1893, a large number of young specimens, hardly one-sixteenth inch in diameter, were collected, all attached to beech roots.

Histological.

Stem.—The stem arises from the bulbous lower portion and branches very soon in its upward course, and continues to do so until it reaches maturity. Its histological characters are very marked and clear. On the outside is a well-defined row of epidermal cells colored reddish brown. The cells are generally nearly round, being but little flattened on either side. Going inward we reach a cortical parenchyma, which is quite thick, consisting of large parenchyma cells with numerous intercellular spaces. Rays of the pith join these cells, giving a peculiar stellate appearance.

The fibrovascular bundles are arranged in a circle, generally two larger ones followed by a smaller one. They are typical collateral bundles. The phloem consists of a large mass of very thick-walled bast fibers on the outside (Pl. III*b*) and a mass of cambiform tissue, consisting of very thin-walled parenchyma cells (Pl. III*c*). The xylem has several large scalariform ducts; annular and spiral vessels are also present (Pl. III, Figs. 1 and 2). Sieve tissue is entirely absent. These correspond to the three divisions of the bundle made by Chatin (16 ap. 79). The dotted cells in the spaces between the bundles I have not been able to find. The pith is composed of large cylindrical parenchyma cells. The cortical parenchyma and pith are joined by rays, giving the stem a peculiar rayed appearance (Pl. I, Fig. 3). The cortical parenchyma extends between the bundles and anastomoses, with prolongations proceeding from the pith. Glandular hairs are found here and there, composed of two basal cells and the end cell. Stomates are found at irregular intervals, but are rather rare. They are of exceedingly simple structure, being formed of the two guard cells joining the epidermal cells on each side.

The branches are to all intents and purposes exactly like the main stem. The bundles are rather more crowded. Toward the end the cambiform portion of the bundle becomes greatly diminished; the other parts, however, remain very distinct.

Rhizoma.—The stem arises from a lower thickened portion which has been termed a *rhizoma*. This portion differs very markedly from the stem above. On the outside there is, it is true, a similar epidermis, the cells of which, however, are much more elongated, being more of a rectangular form. Inside of this is a mass of parenchyma cells, much larger and thinner-walled than those of the cor-

tical parenchyma of the stem. They are roundish, oval, and do not appear to push between the bundles as in the stem. The bundles are so changed that it is hardly correct to call these aggregations of cells a bundle, but for convenience I shall retain this name. As will be seen from plate IV every vestige nearly of the clear collateral bundle of the stem is lost. At *a* are some of the cortical parenchyma cells; next comes a group of thickened bast cells, *b*. On either side of these, *i. e.*, toward the next mass of bast of the neighboring bundle, is a group of large pitted thickened cells. About the middle of the bundle, at *d*, will be found a large number of tracheids. At *e* is a mass of very small parenchyma cells closely crowded together. They might be compared to the cambiform tissue of the bundle of the stem, although an absolute connection has not been demonstrated. Further inward is a small number of bast fibers, *f*. Another set of tracheids and some more thin-walled small cells complete this curious bundle; at *g* is the pith. Similar cells to those at *b* are here and there between the bundles; others are oblong, with irregularly thickened walls and some irregularly reticulated cells. (Pl. IV, Fig. 1.)

As one goes lower down in the rhizoma the character of the bundle gradually changes. At first the bast stops; the last traces of vessels make way for short, thick scalariform tracheids which begin to send off branches in various directions. The number of seemingly independent cell elements, as sclerenchyma cells, long series of cells thickened in various ways, increase until near to the lowest end of the rhizoma. Here we find nothing but an irregular system of tracheids, the branches of which anastomose constantly. Branches go off to the grapplers and scales, generally consisting of one to three rows of tracheids.

It may not be inappropriate at this point to discuss briefly the justification of the term *rhizoma* for this structure. Gray (29*b*) defines a rhizoma as "a creeping stem or branch growing beneath the surface of the soil or partly covered by it." A little further on (p. 43) he says: "Plants with such running rootstocks are always perennial." For a long time botanists have recognized that certain subterranean parts of plants bearing leaves or homologues of leaves were to be regarded as more nearly related to stems than roots, and in consequence gave such parts the name of rhizoma. A rhizoma has then been regarded as a part having the structure of a stem, differing from it only in appearance and position. When, however,

we regard the rhizoma of *Epiphegus*, which to avoid confusion I shall term the subterranean stem to distinguish it from the aërial stem or true stem, we are at once struck by very marked structural characters which distinguish it from the aërial stem.

In the first place, the subterranean stem appears to be an annual, and would therefore not quite agree with Gray's definition. We have seen what great differences exist between the fibrovascular systems.

The true stem has distinct bundles with bast and long spiral and annular vessels, arranged symmetrically in a ring, separated individually by rows of definite character. On the other hand, the vascular elements of the subterranean stem consist of tracheids; all bast has disappeared, and there is no regularity of arrangement in these tracheids. The differences between the two merge gradually; a complete line of demarcation cannot be drawn.

But we must not alone consider the difference of arrangement of the tissues in the aërial and subterranean stem, but also the organization or structure as a whole—a point of view quite as important if not more so than the first, as regards the philosophy of the point in question. The organization rises as we pass from the subterranean stem to the true stem in correspondence with the separate elements. In the subterranean stem the vascular element is the trachea, and the fibrovascular element, so called, which alone is present in the stem, is lacking absolutely in the rhizoma or subterranean stem. As we go higher the bundle becomes more and more differentiated, the individual elements are more distinct, until we reach the perfected bundle of the true stem. Again, this structure bears scales at various points and has branches arising from the axils of these scales, stamping the whole as a stem structure.

Before making final conclusions as regards this stem I desire to regard the separate elements of the true fibrovascular system more in detail. As has been said, in the true stem we find well-developed annular and spiral vessels; also scalariform vessels. In the subterranean stem these elements have entirely disappeared, the vascular element being represented by short reticulated tracheids. The latter, I think, are universally regarded as the lowest forms of tracheary tissue. (One might refer to their occurrence in the ferns, where they constitute the only vascular representative.) At certain points between the main subterranean stem and the true stem tran-

sitions from annular and spiral vessels to tracheids can be readily seen. Plate IV shows such a case. The annular vessel *a* becomes irregular toward its lower end. It merges over into the irregular scalariform vessel *c*. This, at its lower end, runs over into the tracheid *d*, which continues into the series of tracheids *e*, *f*, etc. The scalariform vessel *b* continues further on before changing. In this way, no doubt, numerous other vessels could be traced.

We now come to the point where we can ask what is the meaning of all this difference between the lower part of our plant and the upper stem. As an explanation, I would say that the subterranean stem had been reduced in structure in the course of time because of its immediate function, namely, that of taking nourishment from another plant. In it we find the simplest structures, the simplest bundles. The tracheid is, as has been said, the lowest form of vascular tissue, and besides it we find only parenchyma and a few irregular forms. Had the plant remained an independent plant (as we may suppose it once was) there would without doubt be vessels and bast developed. There has been a degeneration throughout, because there was no longer any necessity for the functions exercised by more highly organized structures. The roots have degenerated to the grapplers, of which more will be said further on. With various modifications, I think this explanation will fit the case. Hence we may safely regard the subterranean stem as a very primitive and much reduced *rhizoma*.

Grapplers.—The rhizoma of *Epiphegus* is covered all over by twisted and branched structures called *grapplers* by Fergus (24). Gray has called these structures roots, and even if they have not the structure in general of true roots, yet I think they undoubtedly act as true absorbing organs. They serve also to fix the plant in the ground and attach it to its host, being admirably adapted to these functions in being stiff and capable, as it appears, of fitting themselves closely to any object they happen to strike. I had occasion to note the great difference in the development of these grapplers in respect to length and number in different soils. In Delaware county on the side of a hill the humus of the beech woods was very thick, consisting of dead and decaying leaves in layers. The whole was very soft and easily moved about; consequently, to hold the plant in upright position, a large number of grapplers were thrown out, which pierced the leaves in various directions, holding them in po-

sition. In Garretsons, Staten Island, I noticed that the conditions were very similar to those just described, and also that the grapplers were well developed. In Six Mile creek, Ithaca, where the soil was more compact and not so loose, the plants had only a few grapplers, the soil being hard enough to hold the rhizoma without very much extra support. Their power of fitting themselves to the host root is something remarkable. One would imagine that these organs in their young stage were perfectly straight. Two explanations for their curved condition could be given. One is that, being long and straight, they coiled around the root on touching it; the other, which seems the more probable, is that when very young the grappler touched the root and began growing around it. I found it impossible in some cases to remove the grappler from a root by slipping it off; it adhered so tightly to the same that it had to be cut. Perfectly straight grapplers or even straight branches are very rare; all are, as a rule, curved or twisted in various ways.

Structurally they are very simple organs. A root-cap is entirely wanting, as are most of the other elements of roots. The vascular system is represented by a series of tracheids, generally one or two rows. These extend nearly to the tip of the grappler (Pl. Va). The remaining tissue is entirely parenchymatous, and consists of very large oblong cells *nearly filled with protoplasm, each showing a nucleus*. It is this fact, namely, the large amount of protoplasm in the cells, especially near the tip, that leads me to think that these organs are more than structures used for support. Cells not engaged in active work of absorption or assimilation as a rule do not contain protoplasm to such an extent and show such well-developed nuclei as these do. To what extent the function of absorption may be ascribed to the grapplers is something I would not like to say, but one would suppose that at least water would be taken in, and perhaps organic salts. But, whatever this absorption may be, it certainly is but very slight, else why this great degeneration of structure in an organ apparently homologous to the roots of self-sustaining plants? (Pl. V, Fig. 6.)

Scales.—On the rhizoma, stem, and branches are found small scales, the reduced leaves of the plant. These organs are similar to the other reduced parts in being very simply constructed. On Plate V, Fig. 1, is represented a transection of one of these scales near its base. A well-developed epidermis covers the outside.

Five fibrovascular bundles are present—a central large one, a smaller one on each side of the central one, *b*, and two others beyond these, *c*. The central bundle is represented enlarged at Fig. 2. It will be seen to consist of three parts, like the bundles of the stem, of the phloem, consisting of several large bast fibers (seven in this case), the central cambiform portion of thin-walled cells and the xylem which, however, instead of being formed of long vessels is made up of tracheids. This completes a good collateral bundle. One of the bundles represented at *b*, Fig. 1, is seen enlarged at Fig. 3. This has no bast whatever, consisting of cambiform tissue, *b*, and tracheids, *c*, the latter constituting the xylem. One of the bundles, *c*, Fig. 1, is shown at Fig. 4. This is the most reduced of all, being made up of but a few tracheids.

In these bundles will be seen an interesting example of reduction of parts from loss of function. The scales may be considered as the former leaves of the plant when this was still independent. These leaves acted as the assimilating organs, and were consequently highly organized, having an extended and well developed fibrovascular system, chlorophyll, and numerous stomates. When the plant changed its mode of life the leaves were no longer compelled to assimilate; an extended vascular system was no longer necessary; so with each succeeding generation of plants the leaf surface was reduced, the vessels gradually disappeared, the lower forms, the tracheids, taking their place.

As one approaches the tip of the scale each bundle assumes a simpler form, losing one of its elements. Pl. V, Fig. 5, shows a diagrammatic representation of the bundles. The central bundle at the tip of the scale is like one of the outer ones. The bundles, *b*, are so also, consisting only of tracheids. The main branch comes from one of the bundles of the stem, the vessels of the latter changing gradually into tracheids similarly to the process in the rhizoma. Stomates are found here and there upon the scales, especially the outer side, but they are rather rare.

From the earliest stages nearly all the cells, no matter where they are, will be found filled with irregular starch grains. The rhizoma and stem are particularly full of starch, the cells being filled entirely. At the time of flowering the calyx of the flowers and bracts around it are found to contain starch in abundance. So much is conveyed into these parts that a large quantity may still be found after the fruit has been fully ripened.

*Fagus Ferruginea.**Systematic.*

Our common beech is a large, stately tree, with a light bark and hard wood, and is highly esteemed because of the latter. It is common throughout the eastern part of the United States, with its center of development on the bluffs of the lower Mississippi. The distribution is given thus (65): Nova Scotia and the valley of the Restigouche river to the northern shores of Lake Huron and northern Wisconsin, south to western Florida, west to eastern Illinois, southeastern Missouri, northeastern Arkansas, and the Trinity river, Texas (Pl. X). It will be seen from the map that the distribution of *Epiphegus* and *Fagus* agrees nearly in every point.

Histological.

From the structural point of view, we are concerned only with the root of the beech. The normal root (Pl. VI, Fig. 1), has a well developed cortical portion, *e*, the cells of which are being worn off and new ones developed below. Going inward we find the phloem portion, consisting of several highly refracting bast fibers, *d*, and a layer of parenchyma cells, which are somewhat compressed and stained deep blue, the cambiform tissue, *c*. Between this and the xylem is situated the cambium layer, *g*. The xylem, *b*, consists of long woody vessels of varying size. The pith, *a*, consists of angular and strongly lignified cells. In all roots examined secondary thickening had already taken place, thus destroying the radial type of bundles. The medullary rays, four or five in number, are very striking, *f*.

Near the parasite this type of root is changed in a remarkable manner. A portion of this root in longitudinal section is seen in plate VI, Fig. 2. The xylem portion of the root is reduced to the small band at *b*. What appears to be cortex has enormously developed, so that a large part has been compressed, *c*. Outside of this is the true cortex or bark, consisting of numerous small cells, *d*. The same is seen on plate VIIc, where the bast has entirely disappeared and the cortical parenchyma, *m*, has become very thick. What the cause of this abnormal development may be can only be conjectured, but I am inclined to ascribe it to some chemical irritation caused by the parasite stimulating the formative layer around the bundles to form this mass of tissue.

Connection of Epiphegus and Fagus.

After having discussed the structure of the haustorium of *Orobanche*, Koch (39c) concludes with these words; "That the whole anatomical structure of the haustorium and the host, and especially in its advanced stages, is extremely complicated and cannot be explained without embryological study, will appear from the foregoing. From the completed structure one might just as well believe that the haustorial body was a single axis into which the tracheary tissue of the host had grown. . . . With the *Orobanches* the parasite alone is aggressive, pushing into the tissue of the host. The latter, it is true, assists growth at the junction of the haustorium by common growth, which leads to the formation of the intermediate organ, causing the union of the several channels carrying food products."

As respects the complicated condition of the mature haustorium of *Orobanche*, the same can be said for that of *Epiphegus Virginiana*. In beginning the study of the connection it was believed that the host grew into the parasite, and from all appearances it still seems to be so. Koch has found that for *Orobanche* this is not the case, and it would appear reasonable to suppose the same would also be true of *Epiphegus*.

Before describing the connecting point between the two I would note some of the effects which are due to the parasite on the beech root. In the description given above of the abnormal root it was seen that the cortical parenchyma developed enormously. Such changes in the structure of the beech root are met with in most cases. The modification is not limited to the parts close to parasite, but extends for two inches or more from the point of union. Not only is the root on which the *Epiphegus* is growing changed, the main root from which it springs also undergoes modification. It begins to swell some distance before reaching the point where the smaller root branches off, the swelling increases and reaches its maximum directly opposite the smaller root. From this point outward there is a marked falling off in size and often complete decay an inch or so from the smaller root. Such a case is represented on Pl. II, Fig. 2. The part "*a*" is nearest the trunk and is normal in structure. At "*b*" a rootlet comes off to which an *Epiphegus* was attached. It will be noticed that the main root is thickened at

"*b*." From this point it becomes smaller, and at "*d*" is scarcely half the normal size. Sections made at points C-D, E-F show that the increase is due to the development of cortical cells of irregular shape and of large size forming a somewhat spongy tissue.

On the side away from the parasite the root has nearly its normal structure. A small ring of irregular cells, generally about twice as long as broad, the long axis toward the pith, is found outside the true wood; but as we come around toward the rootlet "*c*" this spongy tissue is very much increased. Immediately outside the pith are a few woody fibers, followed by the spongy parenchyma. The pith comes to occupy a somewhat eccentric position, with a larger amount of wood on the side away from the parasite. These changes are no doubt due to some chemical action of the latter. The smaller roots are affected similarly, though in not so marked a degree. (See Pl. I, Fig. 2, rootlet between "*a*" and "*b*," from which a part of the cortex has been removed.)

These attachments show, furthermore, how completely the intruding plant takes up the root which it attacks and causes neighboring roots to absorb for it. It seems very probable that the young parasite in its development diverted the flow of sap from its regular course into its own vessels. In the course of time the entire current entered the parasite. Thus the part beyond the attachment, no longer receiving nutriment, lost its power of absorption, the cells degenerated and finally decayed. It is probably because of this that the parasite seems to be growing, as it does in so many cases, at the end of the root. Pl. II, Fig. 1, "*c*," Fig. 2, "*d*," represent cases in which the root is beginning to disappear, having diminished perceptibly in size.

As has been said above, the structure of the mature connection is extremely complicated. The vascular tissue of the beech root appears to enter the tissue of the parasite and join the vascular tissue of the latter. At a certain point in the root (before reaching the parasite) elongated tracheids appear. There is some doubt whether these are beech or *Epiphegus*. These tracheids are about twice as long as broad, and rapidly increase in number as one approaches the parasite (Pl. VII). At a point opposite the lowest portion of the rhizoma these tracheids make a sharp turn and extend at right angles into the parasite. The cortical parenchyma (Pl. VII*m*) accompanies the same. (In the drawing the root is repre-

sented at the bottom of the page, the end “*o*” being nearest the tree.)

On entering the tissues of the parasite these tracheids appear to meet a number of strands of tracheids nearly isodiametric at a point (Pl. VII, *e*. From this it will be seen that one would be perfectly justified in assuming that the beech enters the parasite. The long tracheids might be called beech tracheids, the shorter ones *Epiphegus* tracheids; but it has been found that two kinds of tracheids in the same plant were not infrequent. The apparent entrance of the beech is made more striking by the complete union of the tissues of both plants. There is no rupture of epidermal cells, the cells of one fusing with the cells of the other. Again, the small parenchyma cells of the lower portion of the rhizoma join with a mass similar to them in the part apparently beech. From the plate it will be seen that there is a portion, *i, g*, which seems to be neither true beech nor true *Epiphegus*. I would call this the “intermediate organ” which Koch has found in the *Orobanches*. Concerning the union of the host and parasite and the formation of this part, he says (39c), page 75: “The modification of structure and consequent growth of the parenchyma tissue cannot be regarded as an effort on the part of the host to exclude the parasite forcibly; the root, moreover, acts, assisting the union with the *Orobanche*, as if nourishing a graft. An intermediate structure is thus formed by the root of the host forming a connecting link between the *Orobanche* and its host. The principle underlying the formation of this middle portion is to enable similar cells to be joined, at the same time allowing the growth of both parts.

“We have herewith the very peculiar case of two plants living together, one of which takes, the other furnishes—a case which cannot be well compared with the well-known cases of symbiosis, in which the mutualism of two plants is of advantage to both.”

The structure of this part in the present case will appear more nearly that of the beech than of *Epiphegus*, and may be supposed to have developed from it. What each part represents I am unable to say for the present, and do not believe it can be explained without embryological study. A distinct epidermis, as is found in the normal root, is wanting, the outer row of cells of the distinctly parenchymatous cortex performing that function. The tracheids on the inside no longer form a complete vascular ring, but are

divided into groups, surrounded by numerous small cells closely packed together and filled with starch. (Pl. VIII, the tissue on the outside surrounding the transformed root is a portion of the parasite which is beginning to join it, as shown in Fig. 1.)

Further along the root becomes surrounded by the parasite, the latter crowds between the two vascular groups (Pl. VIII, Fig. 2). The dotted cells found distributed throughout the rhizoma appear in groups. As the root advances its identity is lost more and more. The cortex is so modified as to resemble the parasitic tissue; tracheids of *Epiphegus* join those of the beech, and both tissues fuse intimately. The general position of the vascular tissue of the beech may be distinguished (Pl. IX*a*); the original medullary rays are still distinct (Pl. IX*m*); perhaps some portions of the cortex. Some distance from its entrance one can no longer discriminate accurately between host and parasite.

A sure explanation of the condition can only be made by studying the early stages. It seems very probable that the relations of the two plants will be similar to those existing in other cases between host and parasite. The apparent entrance of the beech root will be shown to be due to the mode of entrance of the parasite and the complete appropriation ultimately of the whole root by the parasite.

Methods.

The plants which were used in making this study were collected in Fleischmanns, Delaware county, New York. Great care was used in digging them in order to avoid breaking off the host root. The humus was cut on all sides of the parasite; the whole piece was carefully lifted from its place and placed in a collecting box. The soil and foreign particles were washed off by directing a fine stream of water from a hydrant upon the mass. The roots not desired were cut off and the specimens were preserved in 82 per cent. alcohol.

In order to ascertain the general character of the connection of the two plants gross dissections were made. The grapplers were removed one by one, and small pieces cut off with a razor. For the more exact work the parts which were to be studied were put into a Schultze's dehydrating apparatus (see "Collodion Method in Botany," M. B. Thomas, Proc. Am. Soc. Mic., 1890). A large round glass museum jar, 12 by 9 inches, was used, in which tubes with a chamois leather bottom were suspended in 95 per cent.

alcohol; 50 per cent. alcohol was put in the tube with the material, generally in the evening. The next morning the specimens were perfectly dehydrated. They were then transferred to a 2 per cent. solution of collodion (2 grs. guncotton, 50 cc. alcohol, 50 cc. sulphuric ether). In this they were left for from four or five hours up to a day and night. About six hours appeared to be a sufficiently long time. The tissues were then put five to six hours into 5 per cent. collodion (5 grs. guncotton, 50 cc. alcohol, 50 cc. sulphuric ether). They were then imbedded in collodion on corks, the collodion being hardened in 82 per cent alcohol. After six to eight hours the tissues would be ready for sectioning.

A sliding microtome was used, and in all cases (excepting where sections were entirely alike, such as transections of a stem or normal root) serial sections were made. The writer believes that in so doing relationships between different parts were more clearly traced, and points which might have appeared obscure were easily explained. In making the sections the knife was wet with alcohol and a slow cut was made. Rapid sweeps of the knife were tried, but did not give such good results as the slow motion. The sections were put on slides coated with albumen (see "Notes on albuminizing slides for the more certain fixation of serial collodion sections," S. H. Gage, *Proc. Am. Soc. Mic.*, vol. XIII, p. 82). It was found that in coating the slides with albumen the sections adhered much more firmly than they did to non-albuminized slides. After cutting six or eight sections they were stuck to the slide by placing a drop of ether near them, which dissolved the collodion. This method gave better results than blowing the ether vapor, as is often practiced.

Since most of the tissues studied contained large quantities of starch and were much lignified, they had to be treated with some reagents to remove the starch and bleach them. For this purpose the slide was covered with a strong solution of potassium hydrate, which was left on the slide five minutes at the most; generally two to three minutes. The sections were then thoroughly washed with distilled water, and then some Javelle water was added. This was left on until the sections were nearly transparent; then it was washed off with distilled water. Thorough washing appeared very essential to secure a complete stain.

Various stains were tried—aniline stains, hæmatoxylin, and eosin. Hæmatoxylin gave the most satisfactory results. Directly after wash-

ing off the Javelle water the hæmatoxylin was put on and left on for from two to ten minutes. Highly lignified tissues, such as the sections of the beech roots, stained but slightly. Beautiful contrasts were made between the meristematic and cambiform tissues, which stained deep blue, and the bast and woody fibers, which stained but very little. After staining, the sections were thoroughly dehydrated with alcohol; 95 per cent. was found to be of sufficient strength. After dehydrating, the sections were cleared with a clearing mixture, consisting of two parts of crystals of carboic acid added to three parts of turpentine. This worked perfectly in all cases: The sections were then mounted in xylol balsam.

The drawings were made with the aid of an Abbé camera lucida. The Zeiss and Reichert microscopes were used for study.

Conclusion.

In concluding this study of the mature *Epiphegus Virginiana*, I would state some of the problems which need further solution. In the first place, the results so far go to show how true Koch's statement regarding the complexity of the mature connection and haustorium is. Embryological studies alone will be able to explain many of the points which now appear so strange. To that end experiments have been started to germinate some seeds and grow the young stages of the plant. An apparatus devised by Koch (page 2), with some slight modification, is used. Beech seedlings about one year old were planted in the upper part of a cylinder two by three inches in diameter, the earth being supported by a diaphragm with holes in it. The lower portion is kept very moist. The roots of the beech are expected to grow into this lower chamber, and seeds of *Epiphegus* will be placed near them—similar to Koch's experiments with *Orobanche* seeds on *Vicia fava*.

In the second place, I have not been able to completely satisfy myself as regards the function of the grapplers, and, thirdly, as to the variability in the sterile flowers. Where there are numerous grapplers one will generally find numerous sterile flowers and *vice versa*. Whether these two points are in any way connected and what governs their appearance is a point which needs further study.

It is only when these questions have been solved that we will have a true understanding of the relations of *Epiphegus Virginiana* and its host.

Bibliography.

1. Aiken, W. F. : Flora of Maryland, 1837.
2. Austin, — : *Epiphegus Virginiana*, var. *Rauana*, Austin, Bulletin Torrey Botanical Club, vi, p. 65, 1875.
3. Baillon, H. : "Histoire de Plantes," Tome X. Monographie de Bignoniacées et Gesneracées.
4. Barnston, Prof. J. : Flora about Montreal, 1859.
5. Barton, W. P. C. : Compendium of Flora of Philadelphia, vol. ii, p. 50, 1818.
6. Beck, Dr. Günther, Ritter von Mannagetta : Monographie der Gattung Orobanche, Cassel, 1890. (In Bibliotheca Botanica, von Dr. Chr. Luersen and Dr. F. H. Haenlein, Heft 19, Bd. iv.)
7. Bentham and Hooker : Genera Plantarum, vol. ii, p. 980. "Orobanchaceæ."
8. Beyerinck, M. W. : "Wurzelknospen," Verhandlungen der königlichen Akademie von Wetensch. Deel 25, Amsterdam, 1887, 150 pages, 6 pl. (Justs Jahrbücher, vol. xv, i, p. 309, concerning *Orobanche* buds.)
9. Bonnier et L. Mongin : Recherches sur le respiration des tissus sans chlorophylle. Extr. des Ann. de Science Nat. Bot. 6e series, 1884, T. xvii, pp. 293-382, avec 2 planches.
10. Bowman, J. E. : "On the Parasitical Connection of *Lathræa Squammaria* and the peculiar structure of the subterranean leaves." Linn. Soc., Transactions, vol. xvi, pp. 399-420, 2 pl. (1833).
11. Burlius, Th. A. : Compendium of Flora of Wisconsin, 1876.
12. Bush, Frank : Flora of Jackson County, Mo.
13. Candolle, A. de : (a) "Monographie des Orobanches." 1 vol. in 4 to., Geneve, 1827, avec 16 planches. (b) Physiologie Vegetale, 1832, p. 1401. (c) Prodromus Syst. Veg., vol. xi, p. 4.
14. Caspary, R. : "Über Keimung, Species und Nährpflanzen der Orobanchen." Flora, vol. 37 (1854), No. 37 and 38, p. 587 *et seq.*, tab. 3.
15. Chapman, A. W. : Flora of Southern U. S.
16. Chatin, Ad. : (a) Anatomie comparée des Vegetaux plantes parasites, 2 vols., 1 text, 1 plates (113). Paris, Libraire J. B. Bailliere et Fils, 1892. (b) De l'appareil special de nutrition des espèces parasites phanerogames. Compt. Rend., 1879, T. 88 I. pp. 108 and 261. (Ref. Justs Jahrbücher, vol. vii, p. 371.)
17. De Bary, A. : Fungi, Mycetoza, and Bacteria, p. 356. (English translation by H. E. F. Garnsey and I. B. Balfour, Oxford, 1887, pp. 525.)
18. Dieterici, Prof. Dr. Fr. : "Die Naturanschauung und Naturphilosophie der Araber im roten Jahrhundert übersetzt aus den Schriften der Lauteren Brüder." Berlin, 1861, p. 180 (see No. 69).
19. Drude, O. : Biologie von *Monotropa Hypopitys* und *Neottia nidus-avis*. Göttingen, 1873.
20. Duchartre, M. P. : Note sur Panatomie de *Orobanche Erygii*. Ann. d. Sciences Nat. Bot., 3e series, T. iv, 1845, p. 74.

21. Edmonds, H. : Elementary Botany. London, 1888, p. 90.
22. Farlow, W. G. : Vegetable Parasites and their Evolution. Proceedings A. A. A. S., vol. xxxvi, 1887, p. 233.
23. Feay, Wm. T. : Catalogue of Plants near Savannah, Ga.
24. Fergus, S. T. : *Epiphegus Virginiana*. Botanical Gazette, viii, p. 154, 1 plate.
25. Fernald, M. L. : Portland Catalogue of Maine Plants, 1892.
26. Fowler, Rev. James : Flora of New Brunswick, 1885.
27. Frazee, L. J. : Indigenous Botany of Kentucky.
28. Gibson, John : Plants on East Coast of Lake Huron.
29. Gray, Asa : (a) Manual of the Botany of Northern U. S., 1890, p. 761. (b) Lessons in Botany, 1890, p. 226.
30. Guignard, M. Léon : Observations sur les Santalacées. Ann. des Sciences Nat. Bot., 7e serie, 1885, T. ii. p. 181.
31. Hallier, Ernst : Phytopathologie. Leipzig, 1868.
32. Homeopathic Recorder, vol. iv, No. 1, 1889, 1 plate. *Epiphegus Virginiana*, history and medical uses.
33. Hovelacque, M. Maurice : (a) Developpement et valeur morphologique du suçoir des Orobanches. Compt. Rend., T. cv, 1887, p. 470. (Ref. Bot. Zeitung, 1888, p. 462.) (b) Sur le developpement et la structure des jeunes Orobanches. p. 530, T. cv; *ibid.*, 1887. (c) Recherches sur Pappareil végétatif des Bignoniacées, Rhinanthacées, Orobanchacées, et Utriculariées. 8vo, 765 p., 611 fig., Paris, 1888. (Ref. Bot. Cent., 1889, No. 16, p. 534.)
34. Jackson, B. Daydon : "On the occurrence of single florets on the root-stocks of *Catananche lutea*." Lin. Soc. Journal, London, xix, 1882, pp. 288-289.
35. Jessup, H. G. : Flora and Fauna of Hanover, N. H., 1882.
36. Johow, Fr. : Die phanerogamen Schmarotzerpflanzen. Grundlagen und Material zu einer Monographie derselben, 11 woodcuts, 39 pp., Santiago, 1890. (Ref. Bot. Centralblatt, vol. 47, 1891, p. 279.)
37. Kamienski, Fr. : Les organes végétatifs du *Monotropa hypopitys*. Mem. Soc. de Sci. Nat. et Math. de Cherbourg, T. xxiv, 1882, p. 1, pl. 3.
38. Klebs, George : Beitrage zur Morphologie und Biologie der Keimung. Untersuchungen aus dem Bot. Institut Tübingen. Bd. i, pp. 536-635. (Ref. Justs Jahrbücher, vol. 13, i, p. 513.)
39. Koch, L. : (a) Samenentwicklung bei den Orobanchen. Pringsheims Jahrbücher für wissenschaftliche Botanik, xi, p. 218. (b) Entwicklung des Samens von *Monotropa hypopitys*. Pringsheims Jahrbücher für wissenschaftliche Botanik, vol. xiii, p. 202, pl. ix-xi. (c) Entwicklungsgeschichte der Orobanchen, mit besonderer Berücksichtigung ihrer Beziehungen zu den Culturpflanzen. Heidelberg, K. Winter, 1887, 8vo, 389 p., 12 plates. (Ref. Bot. Centralblatt, vol. 31, p. 361, 1887.) (d) Die Klee und Flachs-seide. 1880, Heidelberg, K. Winter, p. 191, 8 plates.
40. Koch, M. : Orobanches de la Flore Allemagne. Ann. d. Sc. Nat., 2 serie, vol. 4, p. 361; vol. 5, pp. 34, 82, 146.

41. Linnæus, C. : Species Plantarum, vol. iii, 1, p. 347.
42. Lory, Ch. : Sur la respiration et la structure des Orobanches. Ann. d. Sc. Nat., series iii, T. 8, pp. 158-172.
43. Masse, G. : On the structure and functions of the subterranean parts of *Lathræa squamaria*, L. Journal of Botany, xxiv, pp. 257-263.
44. Macoun, John : Geologic Survey of Canada, 1883.
45. Martius, — : Über die Vegetation der unechten und echten Parasiten, zunächst in Brasilien. Gel. Anz. d. kgl. bair. Acad. d. Wissenschaften, Bd. 14, p. 353. (Ref. v. Mohl, Bot. Zeitung, 1843, p. 497.)
46. Meehan, Thomas : (a) On the Evolution of Parasitic Plants. Bulletin Torrey Botanical Club, vol. 18 (1891), p. 210. (b) *Sarcodes sanguinæ*. Proc. Acad. Nat. Sc., Phil., Pa., 1881, part 2, pp. 160-162. (c) Native Flowers and Ferns of U. S., vol. ii, p. 93. *Epiphegus Virginiana*.
47. Michaux, A. : Flora Borealis Am. Can., 1803, vol. ii, p. 26.
48. Millspaugh, C. F. : Flora of West Virginia, 1892.
49. Mohr, Chas. : Flora of Alabama, 1880.
50. Newberry, J. S. : Flora of Ohio, 1860.
51. Nuttall, Thomas : The Genera of N. A. Plants and a Catalogue of the Species to 1817, vol. ii, Philadelphia, 1818, p. 60.
52. Oliver, F. W. : *Sarcodes sanguinea*. Annals of Botany, vol. iv, p. 303, 5 plates.
53. Patterson, H. N. : Flora of Illinois, 1876.
54. Perkins, Geo. H. : Flora of Vermont, 1882.
55. Pfeffer, Dr. W. : Pflanzenphysiologie. Leipzig, p. 227, 1881.
56. Pfeiffer, J. : C. Linné, Amoenitat acad., vol. iv, tab. ii, p. 351. 1788, Dissertatio Ixv, Fungus melitensis prop. a.
57. Pitra : Über die Anheftungsweise einiger phanerogamischer Parasiten und ihre Nährpflanzen. Botanische Zeitung, 19, 1861.
58. Poulsen, V. A. : Über den morphologischen Werth des Haustorium von *Cassytha* und *Cuscuta*. Flora, 1817, p. 507.
59. Provancher, l'Abbe L. : Flore Canadienne, 1862.
60. Pursh, F. : Description of Plants of N. A., 1814, vol. ii, p. 431.
61. Rafinesque, C. : Monographia Orobanchearum, 1819. (A work unknown to Gray and De Candolle.)
62. Riddell, J. L. : Synop. Flora Western States. Cincinnati, 1835.
63. Sablon, M. Leclerc du : Recherches sur les organes d'absorption des plantes parasites. (Rhinanthées et Santalacées.) Ann. d. Sc. Nat., serie 7e, vol. vi, Bot., pp. 90-117, plates 3.
64. Sachs, J. : Handbuch der Experimentalphysiologie, 1865, pp. 126-131.
65. Sargent, C. S. : Woods of U. S., Jessup Collection, p. 94.
66. Schacht, Hermann : (a) Die Blüthe und Befruchtung von *Santalum album*. Pringsheims Jahrbücher f. w. Bot., iv, p. 1, taf. i-iv. (b) Beiträge zur Anatomie und Physiologie der Gewächse, 1854, p. 171.
67. Schönlund, Selmar : Contributions to the Morphology of the Mistletoe. Ann. Bot., vol. ii, p. 283, pl. xvii.

68. Schrenk, Joseph : Notes on Haustoria of some N. A. Phanerogams. Bulletin Torrey Botanical Club, ix (1884), No. 10, p. 109.
69. Solms-Laubach, Hermann Graf zu : (a) Über den Bau und die Entwicklung der Ernährungsorgane parasitischer Phanerogamen. Pringsheims Jahrbücher für wissenschaftliche Botanik, Bd. vi, p. 589. (b) Über den Thallus von *Pilostyles haussknechtii*. Bot. Zg., 1874, p. 49. (c) Haustorium der Loranthaceen und der Thallus der Rafflesiceen u. Balanophoreen. Abh. d. naturf. Gesell. zu Halle, Bd. xiii, pp. 237-276.
70. Sutton, C. : A description of five British species of Orobanche. Trans. Linn. Soc., iv (1798), pp. 174-188, 1 plate.
71. Tabmer, Elenore : Catalogue of Plants wild in Michigan, 1877.
72. Tracy, S. M. : Catalogue of Phanerogams of Missouri, 1886.
73. Uloth, W., aus Marburg : Beiträge zur Physiologie der Cuscuten. Flora, 1860, pp. 257-273, pl. ii and iii.
74. Unger, F. : Beiträge zur Kenntniss der parasitischen Pflanzen. Ann. des Wiener Mus. d. Naturgeschichte ii, 1840.
75. Vaucher, J. P. : Monographie des Orobanches, 1827.
76. Warming, — : Om rødderne hos *Neottia nidus-avis*, L. Vidensk Medd. fra den naturhist. For. i, Kjobenhavn, 1874, No. 1-2.
77. Weisner, J. : Untersuchungen über die Farbstoffe einiger für Chlorophyll-frei gehaltener Phanerogamen. Pringsheims Jahrbücher für wissenschaftliche Botanik, vol. viii, p. 575.

Plate I.

Fig. 1.—*Epiphegus Virginiana*, showing the thickened rhizoma, the branching stem, the thick rounded cleistogamic flowers, and the longer tube-shaped sterile flowers near the ends of the branches. $\frac{1}{3}$ nat. size.

Fig. 2.—Seedling beech, with a young *Epiphegus* attached to one of its roots at "A." $\frac{1}{3}$ nat. size.

Fig. 3.—Transection of young branch of *Epiphegus*, showing the ring of bundles, and to some extent the radiation of the pith between the bundles. $\times 60$.

PLATE I.

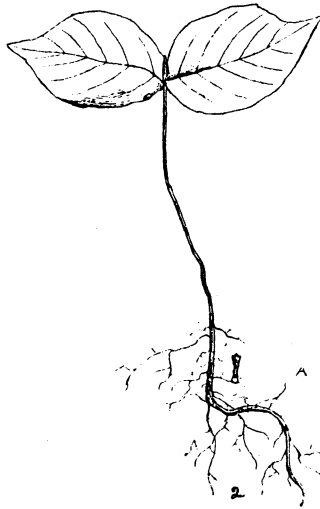
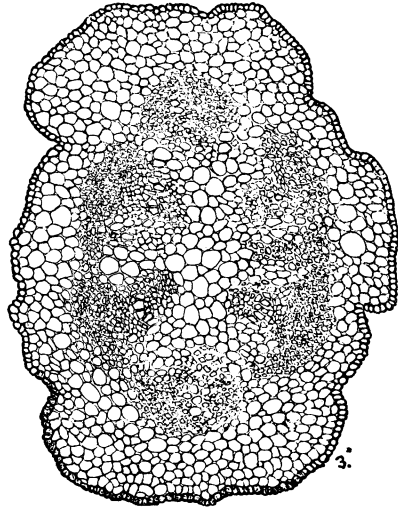
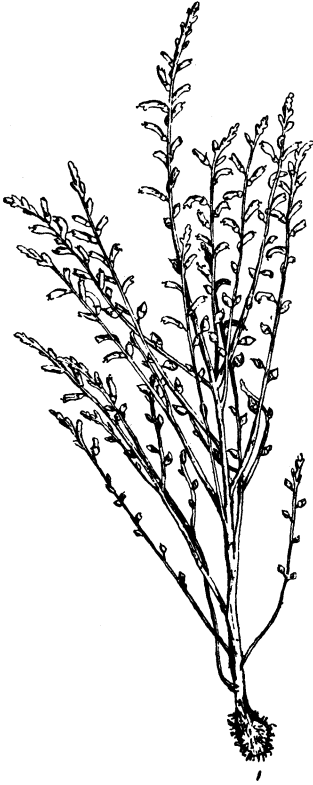


Plate II

Fig. 1.—Lower portion of stem of *Epiphegus*; the grapplers removed and the connection with the beech root shown; *a*, beech root, part nearest the trunk of beech; *b*, connecting point; *c*, part furthest from trunk; *d*, rhizoma of *Epiphegus*. $\frac{2}{3}$ nat. size.

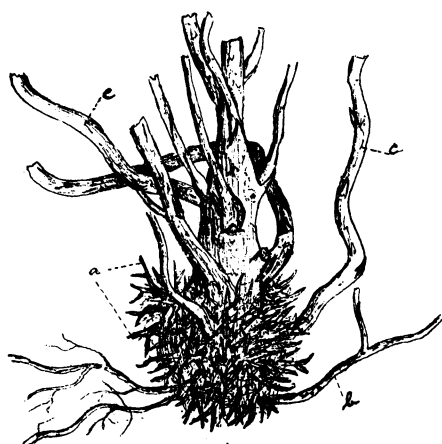
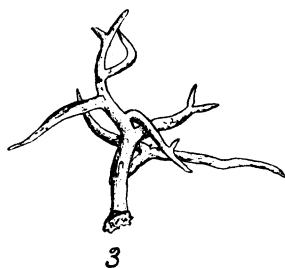
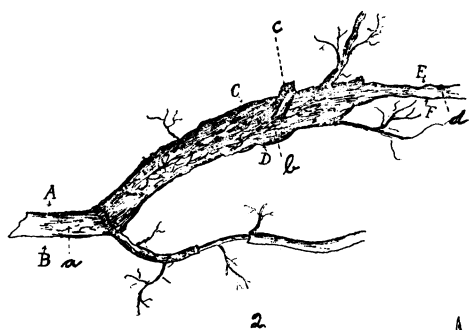
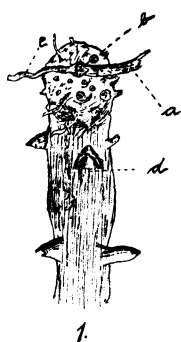
Fig. 2.—Beech root to which parasite was attached. *a*, part nearest the trunk of beech; *d*, part furthest from trunk; *c*, rootlet to which the parasite was attached; *b*, swollen portion of beech root; A B, C D, E F, lines of section. Slightly magnified.

Figs. 3, 4, 5.—*a*, *b*, *c*, Grapplers of *Epiphegus*. Slightly magnified.

Fig. 6.—Rhizoma and lower portion of stem of *Epiphegus*. *a*, grapplers; *b*, beech root; *c*, branches. $\frac{2}{3}$ nat. size.

Fig. 7.—Diagrammatic representation of the vascular system of the rhizoma and beech root. *b*, vascular system of beech; *c*, vascular system of *Epiphegus*. $\frac{2}{3}$ nat. size.

PLATE II.



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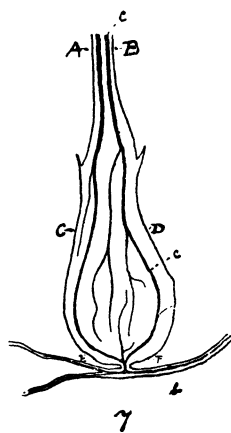
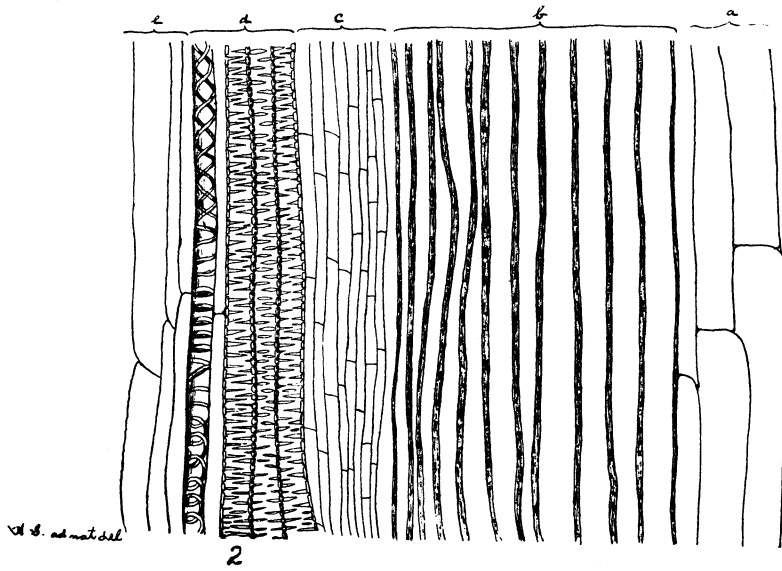
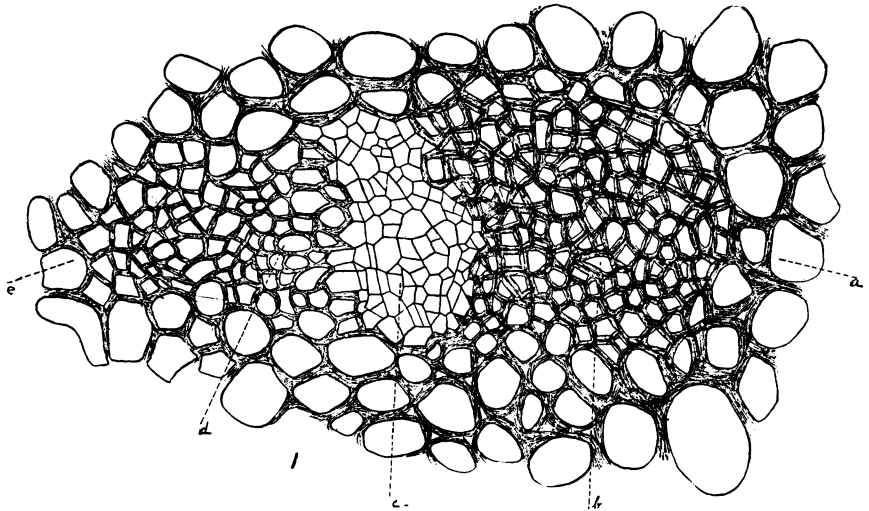


Plate III.

Fig. 1.—Transection of a fibrovascular bundle of the stem of *Epiphegus* (about at the point A B, Pl. II, Fig. 7). *a*, cortical parenchyma; *b*, bast cells; *c*, cambiform tissue; *d*, xylem (vessels and ducts); *e*, pith. $\times 200$.

Fig. 2.—Longisection of similar bundle (lettering as for last plate). $\times 150$.

PLATE III.



ad. mat. del

Plate IV.

Fig. 1.—Transection of a bundle in the upper part of the rhizoma (about C D, Pl. II, Fig. 7). *a*, cortical parenchyma; *b*, bast; *c*, thin-walled parenchyma tissue, staining deep blue with hæmatoxylin; *d*, tracheids; *e*, bast; *f*, tracheids; *g*, pith. $\times 44$.

Fig. 2.—Lower part of stem of *Epiphegus*, showing the transition of a vessel into tracheids. *a*, annular vessel passing over into *c*, reticulated duct; *f*, tracheid joining with the duct *c*; *d*, cells filled with starch; *b*, scalariform duct; *e*, chain of tracheids. $\times 600$.

PLATE IV.

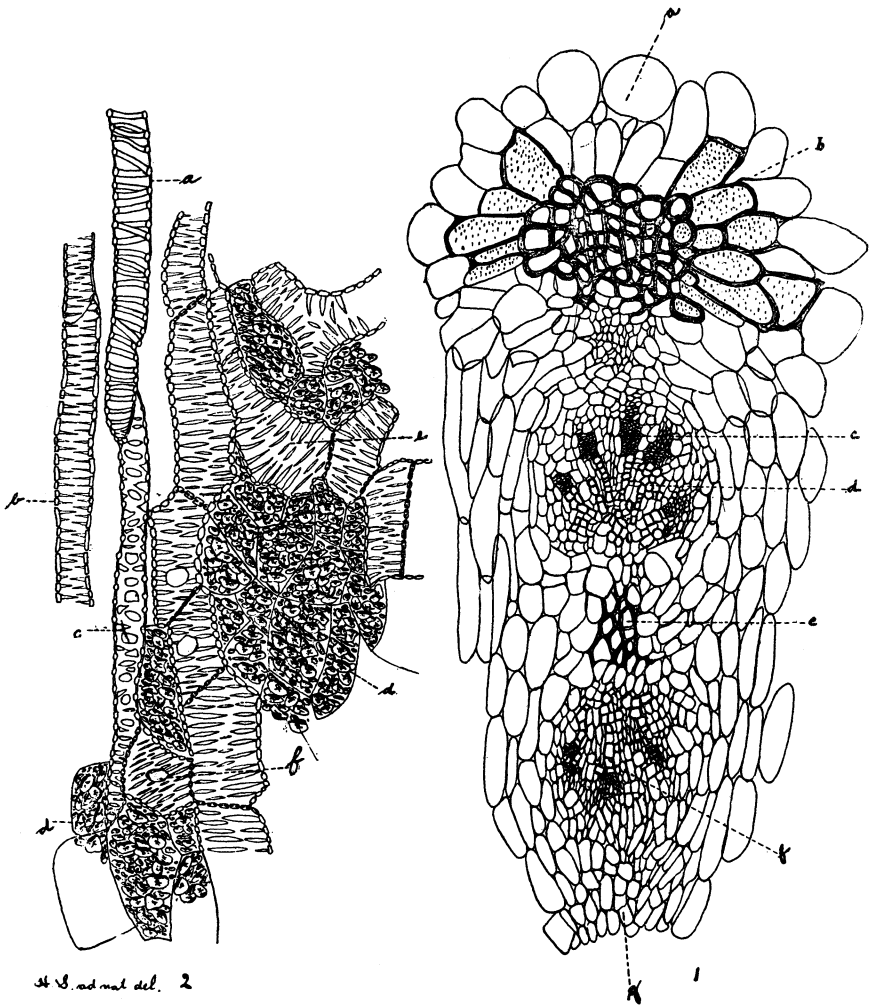


Plate V.

Fig. 1.—Transection of a scale of *Epiphegus* (in the line A B, Pl. IX, Fig. 5). *a*, central bundle; *b*, medium bundles; *c*, outside bundles; *e*, epidermis. $\times 35$.

Fig. 2.—Central bundle enlarged. *a*, bast; *b*, cambiform tissue; *c*, xylem part, consisting of tracheids. $\times 165$.

Fig. 3.—Medium bundle enlarged. *b*, cambiform tissue; *c*, xylem part, consisting of tracheids. $\times 165$.

Fig. 4.—Outside bundle enlarged. *c*, xylem part, consisting of tracheids. $\times 165$.

Fig. 5.—Diagrammatic representation of longitudinal view of a scale of *Epiphegus*, showing the distribution of the bundles.

Fig. 6.—Longisecion of the tip of a grappler. *a*, tracheids; *b*, epidermal cells. All the cells are filled with protoplasm, most of them showing a nucleus. $\times 275$.

PLATE V.

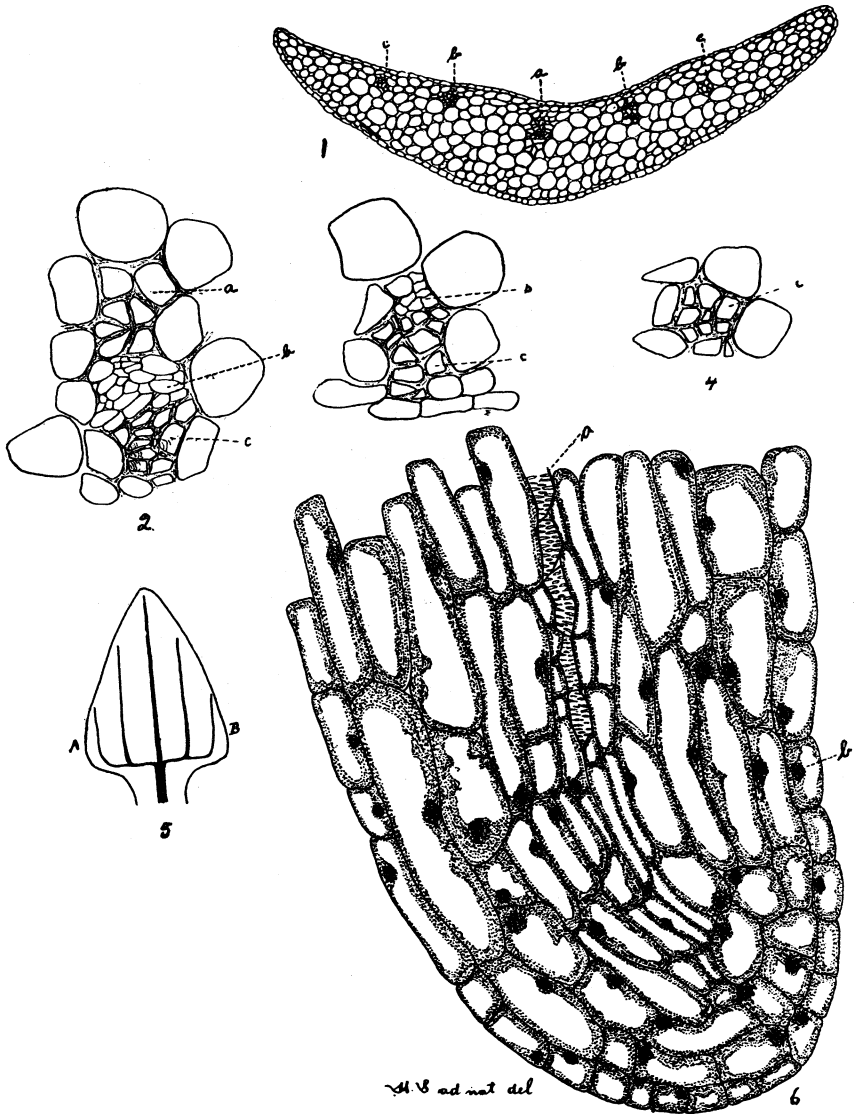


PLATE VI.

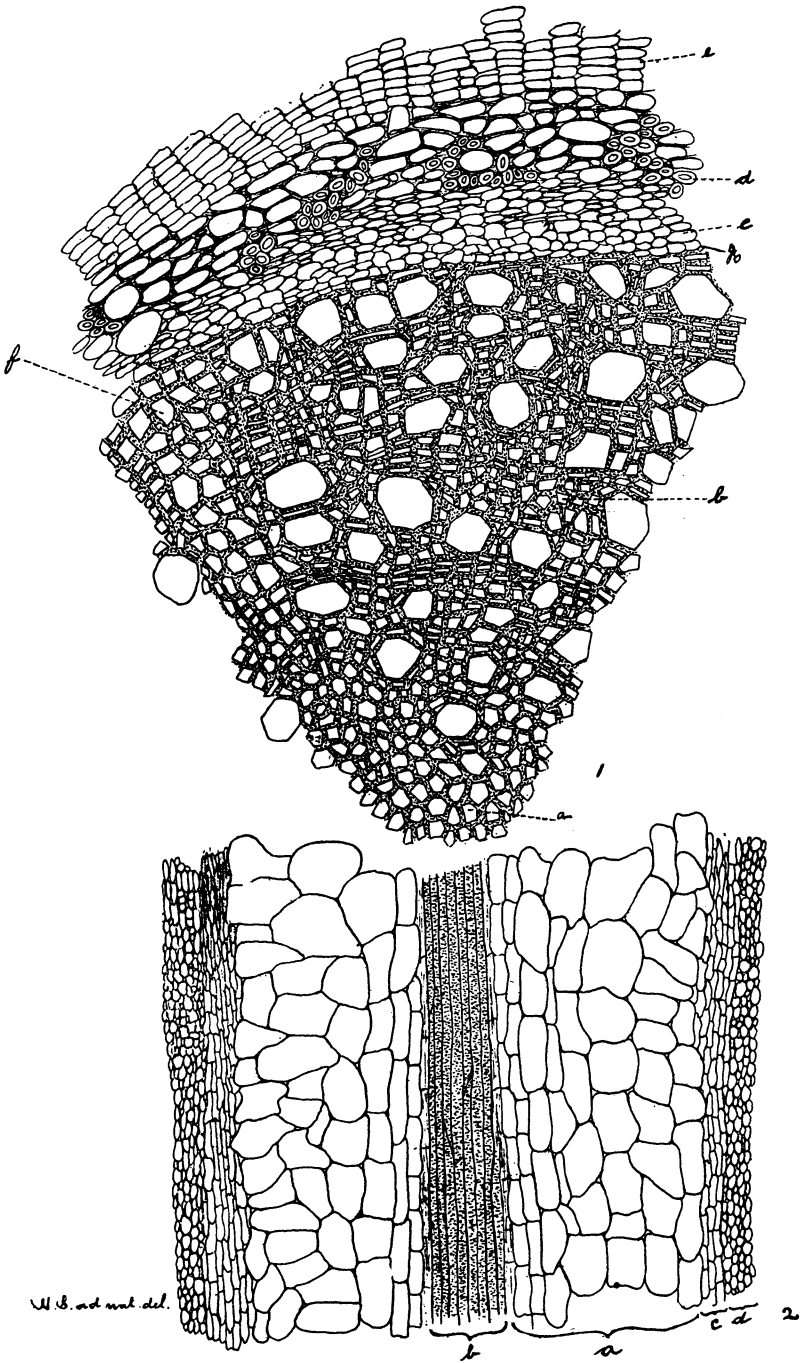


Plate VI.

Fig. 1.—Transection of normal beech root. *a*, pith; *b*, lignified vessels; *c*, cambiform tissue; *d*, bast; *e*, bark; *f*, medullary ray; *g*, cambium layer. $\times 200$.

Fig. 2.—Longisection of abnormal beech root. *a*, abnormal cortical parenchyma; *b*, xylem vessels; *c*, the abnormal cortical parenchyma closely packed together; *d*, bark. $\times 300$.

Plate VII.

Section of connection of *Epiphegus* and *Fagus*, making a longitudinal section of the beech root. *o*, part nearest the trunk of the beech; *m*, abnormal cortical parenchyma; *s*, beech vessels; *c*, bark; *a*, turning point of the tracheids; *g-i*, intermediate organ; *e*, approximate point of differentiation into the two forms of tracheids; *f*, *Epiphegus* tracheids. × 55.

PLATE VII.

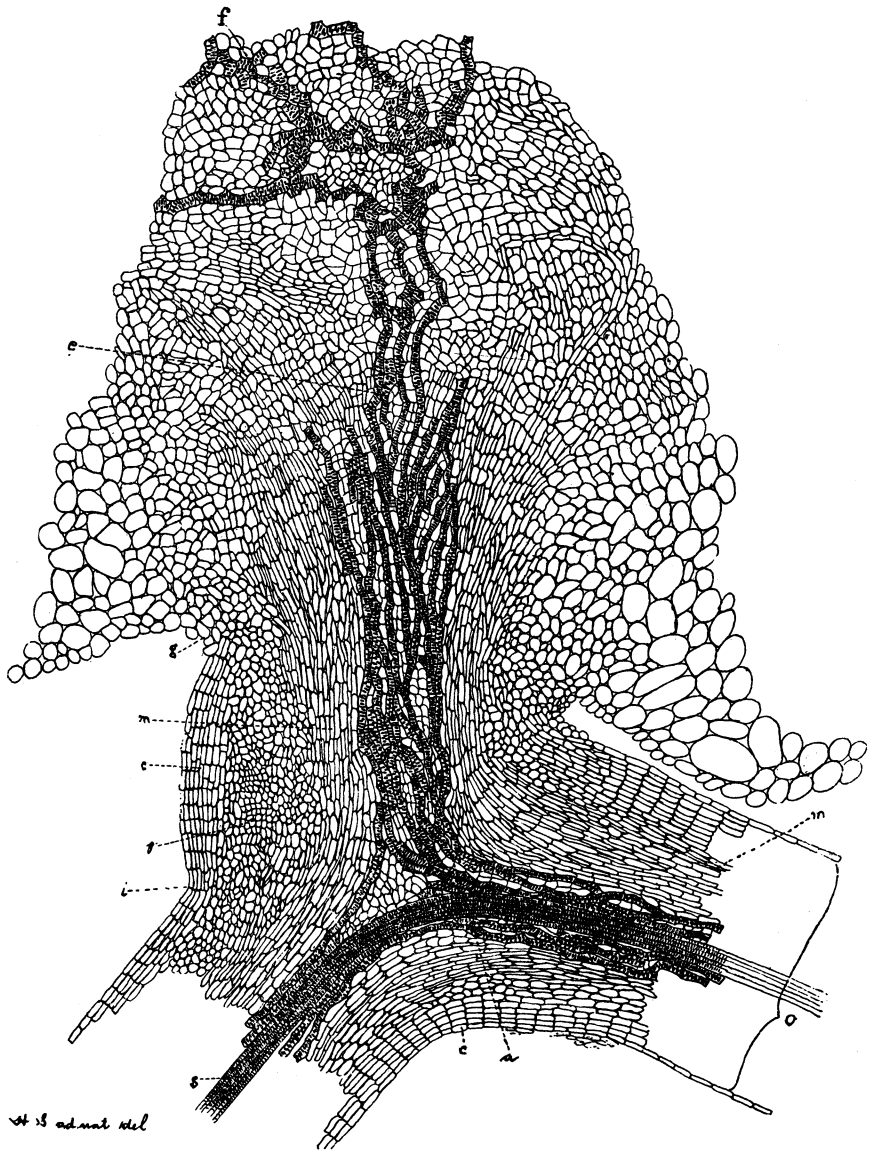
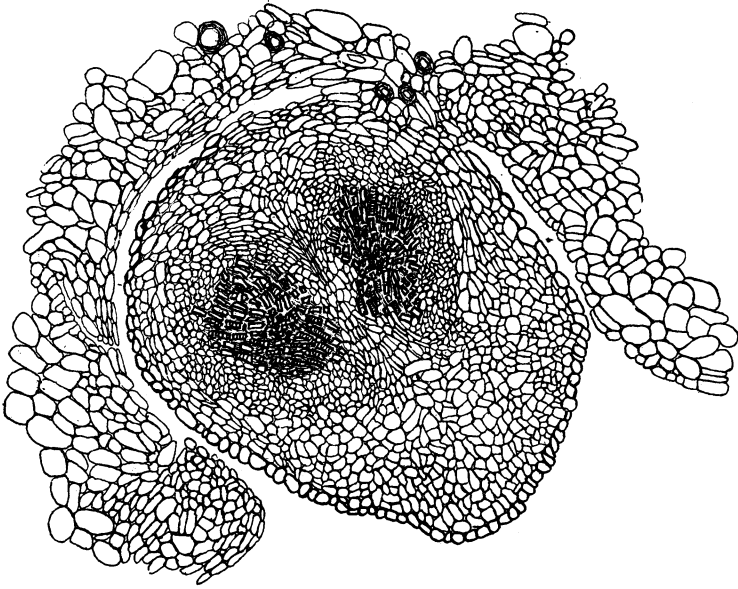


Plate VIII.

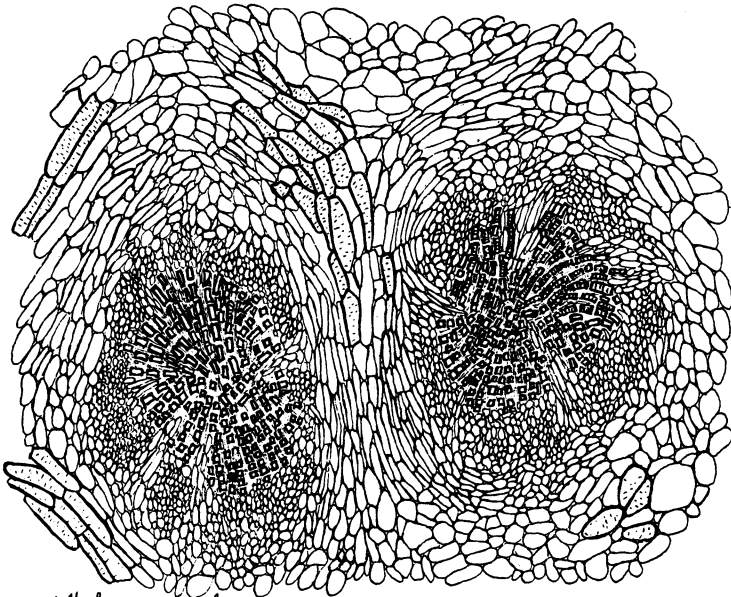
Fig. 1.—Transection of beech root just before entering the parasite. The latter is seen partially enveloping the root. In the former the vessels are collected into two groups. (From photomicrograph.) $\times 70$.

Fig. 2.—Transection of the same root farther in the tissue of the parasite and more disorganized. (From photomicrograph.) $\times 70$.

PLATE VIII.



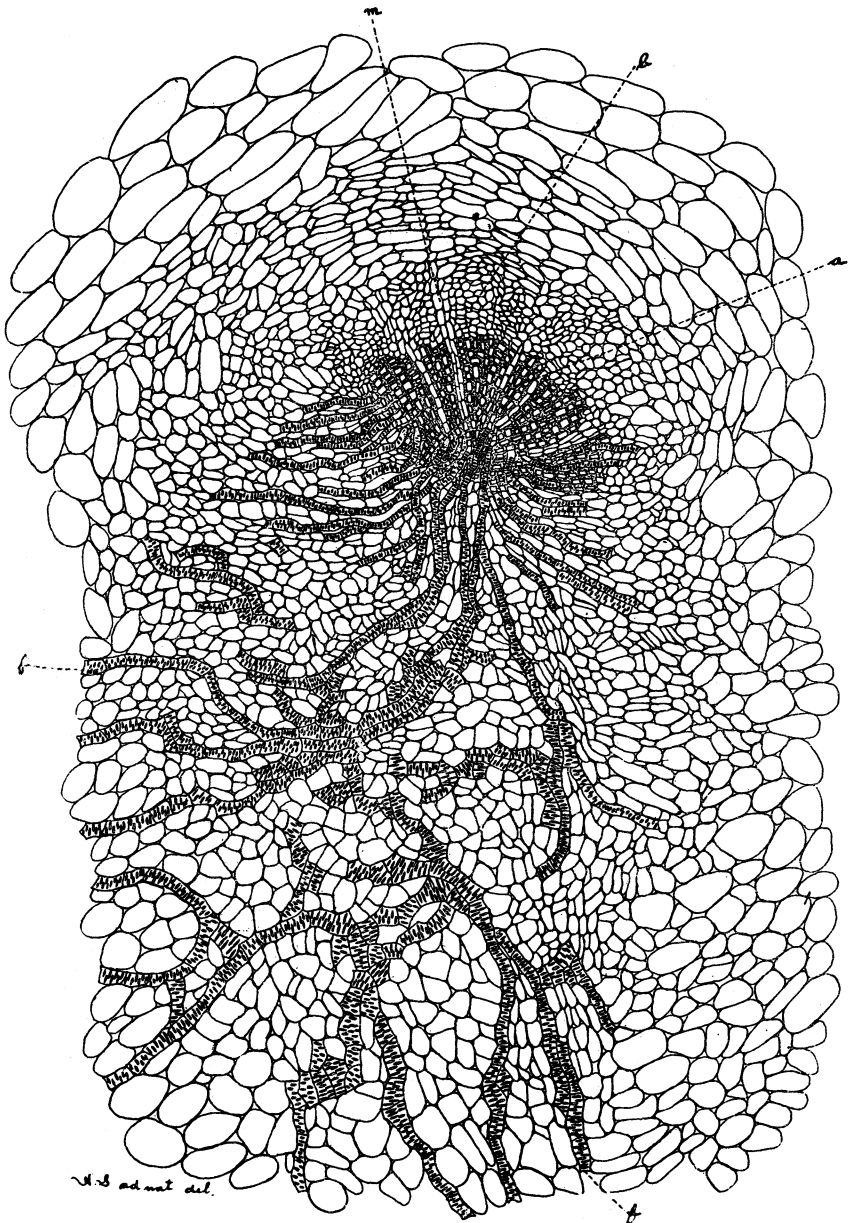
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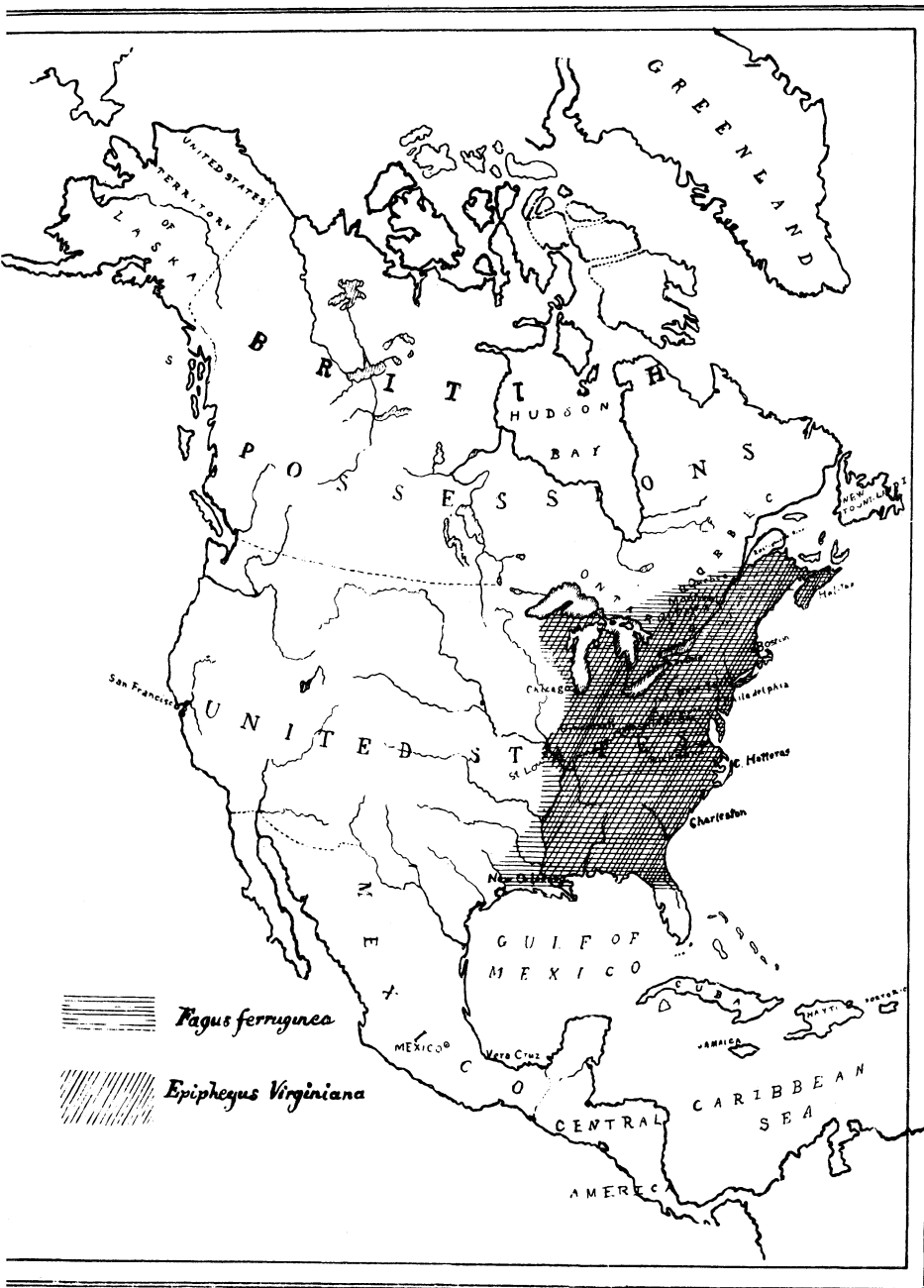
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PLATE IX.



Transection of the connection of the beech and the parasite. *a*, beech vessels; *b*, cortical parenchyma (?); *m*, medullary ray; *f*, *Epiphegus* tracheids. $\times 100$.

PLATE X.



Map showing comparative distribution of *Epiphegus Virginiana* and *Fagus ferruginea*.